Coral Reefs (2005) 24: 157–159
DOI 10.1007/s00338-004-0436-4

NOTE

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Persistence of non-caribbean algal symbionts in Indo-Pacific mushroom corals released to Jamaica 35 years ago

Received: 5 December 2003 / Accepted: 10 March 2004 / Published online: 1 October 2004

Mushroom corals endemic to the Indo-Pacific were collected and brought to Discovery Bay, Jamaica, and released on the fore-reef in the mid to late 1960's by Thomas F. Goreau, an early pioneer in coral research (cf. Goreau et al. 1969 p 180; R. K. Trench, personal communication). Subsequently, the potential problems arising from introduction of an exotic species to the Caribbean were realized. Several attempts to eradicate these non-Caribbean species were then made between 1970 and 1980 and more than 25 adult individuals were removed (cf. Bush et al. 2004; J. Woodley, personal communication). However, re-discovery of two *Fungia scutaria* individuals in March of 2003 showed that a remnant population of this particular mushroom coral has persisted for over 35 years in the Caribbean (Bush et al. 2004). Since being introduced to Atlantic waters, these corals have displayed remarkable resilience, enduring two destructive hurricanes (Woodley 1992), environmental degradation resulting in collapse of native coral populations (Hughes 1994), and several bleaching events related to thermal stress (Goreau 1990).

Understanding the stability and/or flexibility of coral-algal symbioses is of great interest to those concerned with the long-term effects of climate change on reef building corals (Baker 2003). Whether the original symbiont population of *F. scutaria* was replaced by one of the many local *Symbiodinium* spp. found in the Caribbean (LaJeunesse 2002; LaJeunesse et al. 2003) is addressed in this report through use of genetic analyses.

Tissue from a *F. scutaria* collected on the fore-reef (15 m) off the north shore of Jamaica was preserved in 95% ethanol, homogenized, and the DNA isolated as described previously (LaJeunesse et al. 2003). PCR-denaturing gradient gel electrophoresis (DGGE) fingerprinting of the ribosomal internal transcribed spacer region (ITS) 2 was performed and the two lowest and most prominent DNA bands were excised and sequenced (Fig. 1). The genome of this *Symbiodinium* sp. contains two co-dominant sequence variants of the ITS 2. They appear to reflect a phylogenetic transition from C1 (ancestral) to the C1b (derived) sequence. When the DGGE fingerprints and sequences are compared with data from hundreds of Caribbean and Indo-Pacific host taxa, an identical match is made with a symbiont of Pacific origin, type C1b (Fig. 1). That member of *Symbiodinium* clade C was recently identified in the coral *Pavona varians* (collected at 3 m) from the southern Great Barrier Reef (GBR) (LaJeunesse et al. 2003) and in *Leptastrea purpurea* (15 m) and the organ pipe octocoral, *Tubipora musica* (15 m), from mid-shelf reefs on the central GBR (LaJeunesse et al., in press). It is also found in *P. superficialis* (6 m) from the Pacific coast of Panama (A.C. Baker and T.C. LaJeunesse, unpublished data) and appears to possess a wide, albeit uncommon, geographic distribution in the Pacific.

The identical match of the ITS 2 fingerprint, C1b, from the Jamaican *F. scutaria* to samples taken from various Pacific hosts indicates that this *Symbiodinium* sp. is most probably a product of the Indo-Pacific diversification of clade C. Presently, over 50 genetically distinguishable symbiont types, mostly from *Symbiodinium* clades B and C, have been classified from extensive host collections at several sites in the Caribbean (LaJeunesse 2002; LaJeunesse, in press). They predominantly have limited geographic, host-specific and/or well-defined depth distributions within the Caribbean Sea. Only two types from clade C, namely C1 (*S. goreaui*) and C3, are known to also occur within a wide diversity of host taxa

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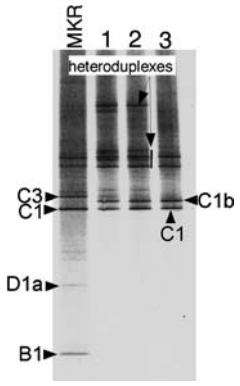

Fig. 1 PCR-DGGE ITS 2 fingerprints of the symbiont found in *F. scutaria* and a comparison with this type identified from various host taxa collected throughout the Pacific. This symbiont is designated by the presence of sequence,"C1b," and distinguishes it from all other PCR-DGGE fingerprint profiles of *Symbiodinium* sp. characterized from the Caribbean (cf. LaJeunesse 2002; LaJeunesse et al. 2003 for further details). *Lane 1* profile of the population isolated from *F. scutaria* collected from Jamaica at a depth of 15 m. *Lane 2* a near identical fingerprint profile from that of the symbiont sampled from the coral *L. purpurea* (15 m, central GBR). This exact same fingerprint was found from *P. varians* (3 m southern GBR) and *P. superficialis* (East Pacific, Panama, 6 m). *Lane 3* C1b from the octocoral, *T. musica* (15 m, central GBR). This last profile displays a similar fingerprint to the Clb found in scleractinians (*lanes 1* and *2*), but while it is scored as being the same symbiont, it lacks several faint diagnostic bands that distinguish it from the others. The marker lane (MKR) is a mix of common symbionts from clades B, C and D. Less stable heteroduplexes, created by the mismatch annealing of DNA strands from the homoduplexes resolved lower in the gel, are indicated.

in the Indo-Pacific (LaJeunesse et al. 2003; LaJeunesse et al., in press). However, a diverse assemblage of clade C "types" distinct from those in the Caribbean has been documented from surveys of symbiont diversity from the eastern Pacific, Hawaii, Australia's GBR, Okinawa, western Indian Ocean, and the Red Sea (LaJeunesse et al. 2003; LaJeunesse et al. 2004; LaJeunesse et al. in press; A.C. Baker and T.C. LaJeunesse, unpublished data). Interestingly, molecular phylogenetic analysis comprising all clade C ITS 2 sequences can be construed in terms of a major radiation spreading from C1 and C3 (the two ecologically different generalists are separated by a single base substitution in the ITS 2 region) (LaJeunesse, in press). The terminal nodes of this radiation are primarily represented by host-specific, regionally endemic (e.g. Hawaii vs. GBR) and/or rare types. These data show that the clade C assemblage from each ocean basin has evolved independently since biological exchange between the Indo-Pacific and Atlantic ended or was seriously restricted during the Miocene-Pliocene transition (Collins et al. 1996; Coates and Obando 1996; Haug and Tiedemann 1998).

There is the possibility that the *F. scutaria* brought to Jamaica acquired C1b 'naturally' from the Caribbean. Three independent surveys of hosts on Pacific reefs have identified type C1b (LaJeunesse et al. 2003; LaJeunesse et al., in press; A.C. Baker and LaJeunesse, unpublished data). To date, no other divergent type evolved from C1 (or C3), possessing a characteristic PCR-DGGE fingerprint, has been found in both the Pacific and Caribbean (LaJeunesse, in press). If C1b were present among Caribbean hosts at similar frequencies, the probability that is has far eluded detection seems low. On the other hand, reef-wide surveys from the South American coast and Netherland Antilles regions are still lacking and hosts there could contain C1b.

Preliminary surveys of western Pacific corals indicate that C1 is the most prevalent symbiont found among hosts that must acquire symbionts from the external environment, i.e. horizontal transfer (LaJeunesse et al. 2003; LaJeunesse et al., in press) The larvae of mushroom corals are also dependent on 'horizontal' aquisition in becoming symbiotic (Weis et al. 2001). Various species of *Fungia* from the GBR, Okinawa, and Red Sea are known to associate, but not exclusively, with symbionts of type C1 (LaJeunesse et al. 2003; LaJeunesse et al., in press; A.C. Baker and T.C. LaJeunesse, unpublished data). Associations with particular symbionts can change in fungid populations over environmental, latitudinal, and biogeographic ranges (LaJeunesse et al., in press). In Hawaii, *F. scutaria* exhibits high specificity for symbiont C1f, one out of the 20 *Symbiodinium* spp. identified from this region (LaJeunesse et al. 2005; Rodriguez-Lanetty et al. 2004). Experiments examining the infection rate and *in hospite* growth of various *Symbiodinium* spp. introduced to aposymbiotic *F. scutaria* larvae suggest that the establishment of symbiosis involves a selective and/or competitive process (Rodriquez-Lanetty et al. 2004). The symbiont type that is most successful at initiating infection and growth within this host ultimately populates the juvenile coral. As reported for some gorgonians, once a symbiont population becomes established, it can remain fixed for the life of the colony/individual (Coffroth et al. 2001; Goulet and Coffroth 2003).

One of the important implications of our findings is that, *F. scutaria* has maintained a symbiont population recorded only from the Pacific despite continuous exposure to indigenous pools of Caribbean symbionts. Since their introduction more than three decades ago, sexual reproduction has probably not ocurred given the low number of individuals (Bush et al. 2004). Therefore the symbiont population in *F. scutaria* apparently has persisted through the direct, 'vertical,' transfer of symbionts that occurs during the asexual budding process. The longevity of this association for so many years challenges a prevailing notion that these symbiotic combinations are all highly plastic and explicitly governed by external environmental factors (Rowan et al. 1997; but see Goulet and Coffroth 2003).

This example also indicates that the geographic origin of a particular coral can be assessed through the identity of its symbiont (T.C. LaJeunesse et al., unpublished data). A previous report argued that the introduced *F. scutaria* were from Eilat, Israel

(Bush et al. 2004). Analysis of the symbiont identity raises the more likely possibility that the parent individual of the specimen we examined originated from somewhere in the Pacific. Goreau was at Lizard Island in 1967 during the Belgian Great Barrier Reef Expedition and reports returning to Jamaica with specimens of *Diaseris* and *Cycloseris* (Goreau and Yonge 1968; Goreau et al. 1969). There is also the possibility that additional collections were made at one of several locations in the central Pacific (e.g. Palau, Guam, and Saipan), also visited by Goreau around this time (N. Goreau and J. Woodley, personal communication). The precise origin of this Jamaican fungid may be determined as more surveys of coral symbionts are conducted throughout the Indo-Pacific and Red Sea. In the future, recovery of natural populations of *F. scutaria* associating with C1b in a region that corresponds with Goreau's travels may further resolve this debate. As this relates to larger issues, a comprehensive phylogeography of *Symbiodinium* ITS diversity could have future application in certifying the collection locations and/or countries of origin for corals in the aquarium trade (T.C. LaJeunesse, unpublished data). Lastly, analyses of zooxanthellae distributions may be of additional importance in delineating genetic connectivity between regions (Santos et al. 2004).

The ecological impact of introducing this Indo-Pacific coral to the Caribbean appears negligible, and with its most recent discovery and removal, *F. scutaria* may indeed be finally 'eradicated' from Jamaica. However, over several decades, these introduced hosts have continuously expelled their symbiont populations into the surrounding environment as part of a natural process (Steele 1977). While there are no known examples of an ''invasive'' coral threatening to take over the ecosystem to which it was introduced (e.g. *Tubastraea coccinea* in the Caribbean, Fenner 2001), the consequences of introducing a new coral endosymbiont to these ecosystems remain unknown.

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